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•研究报告•

基底颜色对两种沙蜥体色变异的影响

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摘要: 生存在不同基底颜色环境下的爬行动物种群通常表现出丰富的体色地理变异，其体色变化的潜在机制具有多样性。变色沙蜥(*Phrynocephalus versicolor*)和草原沙蜥(*P. frontalis*)具有较近的遗传关系，曾被认为与荒漠沙蜥(*P. przewalskii*)组成同一系统发育种组。本文应用光纤光谱仪(AvaSpec-2048)，通过记录沙蜥背部体表12个部位的皮肤光反射率，定量比较在黑化环境下的深色变色沙蜥与非黑化环境下的浅色草原沙蜥自然体色变异，研究其种群体色变异是否具有时间可逆性，并探讨基底颜色对沙蜥体色的影响机制。研究结果表明，黑化生境下的变色沙蜥体色显著深于非黑化枯黄色生境下的草原沙蜥。此外，对黑化与非黑化样本开展的生境互换移植围栏实验，即把枯黄色生境中非黑化的草原沙蜥移植于黑色的基底环境中饲养，把黑化生境中黑化的变色沙蜥移植于枯黄色生境中饲养。结果表明，饲养1周后黑化群体背部6个检测部位的光反射率显著变大，其他部位均无显著变化；而非黑化群体只有左后肢和背部右上方2个部位的皮肤光反射率发生显著变化，其他部位反射率无显著变化。结果表明，变色沙蜥体色变异能力比草原沙蜥强，体色表型可能已经在两个近缘沙蜥物种中稳定遗传，基底生境颜色的短期变化在统计学上能引起肉眼难以识别的轻微的体色变异，个体发育相关的一些遗传因素可能对体色变异起控制作用。

关键词: 黑化；体色变异；沙蜥；皮肤反射率

Effects of substrate color on the body color variation of two agamid lizards, *Phrynocephalus versicolor* and *P. frontalis*

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Abstract: Geographical variation of body color is widely present in reptile populations that survive in different substrate habitats, multiple potential mechanisms can account for this color variation. *Phrynocephalus versicolor* and *P. frontalis*, close genetic relatives, constitute a phylogenetic species group together with *P. przewalskii*. In this study, a fiber spectrophotometer (AvaSpec-2048) was used to record the skin luminous reflectivity of 12 sites across the lizard's body, and we quantitatively compared the natural color variation of dark *P. versicolor* and light *P. frontalis* that lived in "melanistic" and "non-melanistic" habitats, respectively. We aimed to determine whether the color variations of both populations were time reversible, and further discuss potential mechanisms that substrate color may have on color variation of *Phrynocephalus* lizards. Our results showed that the body color of *P. versicolor* in "melanistic" habitat was significantly darker than *P. frontalis* in the "non-melanistic" withered yellow habitat. We also conducted a reciprocal transplantation experiments (i.e. "non-melanistic" withered yellow *P. frontalis* individuals were transplanted and fed in "melanistic" substrate environment, while "melanistic" *P. versicolor* individuals were transplanted and fed in withered yellow substrate environment). For "melanistic" *P. versicolor*, the skin reflectivity of six sites increased significantly after one week, while no significant changes were detected in other sites. For "non-melanistic" *P. frontalis*, except the skin reflectivity of two sites (left hind limb and top right on the

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back) significantly changed, compared to corresponding values one week previously, other sites showed no significant changes. Our results suggest that *P. versicolor* possesses stronger color variation ability than *P. frontalis*, and the color phenotypes are likely inherited in both species. Short-term changes of substrate color can cause slightly color variations that are difficult to distinguish by naked eyes, suggesting ontogeny related hereditary factors may also play a controlling role.

Key words: melanistic; body color variation; *Phrynocephalus*; skin reflectivity

受到自然选择作用，动物能表现出丰富的体色变异，在其避敌、交流等方面发挥重要作用(Barlett & Gates, 1966; Geen & Johnston, 2014)。一些动物的体色会随着所处基底颜色而变化，如头足动物(Hanlon, 2007)、甲壳动物(Hemmi et al, 2006)、鱼(Moretz & Morris, 2003)、两栖动物(Stegen et al, 2004)，以及乌龟(Woolley, 1957)、变色树蜥(*Calotes versicolor*)(蔡波，2014)、变色龙(*Bradypodion taeniabronchum*)(Stuart-Fox et al, 2008)等一些爬行动物。此类体色变化可能与表型可塑性或者遗传因素相关(Vroonen et al, 2012)。

爬行动物的体色变异有两种主要形式：一种是生理体色变化，它是对短期环境刺激的适应，一般通过色素扩散与聚集而快速地实现与基底颜色的匹配(Nery & Castrucci, 1997)；另一种是形态体色变化，这种变化是对长期环境刺激的适应，通常与色素的产量有关(Rosenblum, 2004)。一些爬行动物的生理体色变化可以在几毫秒或者几小时内实现(Thurman, 1988)，而形态体色变化可能需要数天或者数月，并通常受众多遗传因素的影响(蔡波，2014)。

沙蜥属(*Phrynocephalus*)属于有鳞目、爬行纲、鬣蜥科，约有40个物种(赵尔宓等, 1998, 1999)。沙蜥广泛分布于不同自然基底色的开阔生境中，其种群体色表现出丰富的地理变异。变色沙蜥(*P. versicolor*)和草原沙蜥(*P. frontalis*)均属于卵生物种，两者广泛分布于中国北部和西北部，包括新疆、内蒙古、甘肃以及宁夏的荒漠和半荒漠地区(赵尔宓等, 1999)。基于线粒体基因的分子系统学研究认为，分布于新疆及其东部较高地区的沙蜥(变色沙蜥、草原沙蜥与荒漠沙蜥)起源于共同祖先，被视为一个种组(Wang & Fu, 2004)。目前，对该种组的生态学研究主要还是集中于食性(全仁哲等，2006；赵雪等，2013)，繁殖策略(陈强等，1993；郭砺和赵辰光，2001)、两性异形(Qu et al, 2011)等方面，未见有关其体色变异的研究报道。我们在甘肃瓜州县的柳园镇黑山口附近发现的变色沙蜥躯体明显黑化，而与分布在枯黄色生境中的与其近缘的草原沙蜥具有显著的体色差异。由此可见，不同基底色环境下生存的变色沙蜥种组的不同类群是研究动物体色变异机制的良好模型。

近年来，光谱技术开始逐渐应用于动物体色研究(杨灿朝等，2011；杨灿朝和梁伟，2013)，它能对动物体表颜色变化进行量化分析，包括对紫外光、可见光以及红外光区的探测，为生物体体色生态学研究提供了强大的技术支持。不同颜色的皮肤对光的反射率存在差异，黑化的皮肤相对于浅色的皮肤具有更低的光反射率(Porter & Gates, 1969)。本文应用光谱技术，比较了在黑化与非黑化生境下生存的两个沙蜥近缘种(分别为变色沙蜥和草原沙蜥)的体色差异，旨在评估基底颜色对沙蜥体色变异的影响，并采用生境互换移植实验研究两种沙蜥体色变异是否具有可逆性，区分其体色变异的具体类型。

1　材料与方法

1.1　采样、饲养与围栏实验

30条黑化的变色沙蜥成体(15♂，15♀)采集自甘肃省瓜州县柳园镇的黑山口(95.47° E，41.01° N)，海拔1,683 m；30条非黑化的草原沙蜥成体(15♂，15♀)采集自内蒙古自治区巴彦淖尔市乌拉特前旗(108.73° E, 40.75° N)，海拔1,080 m (图1)。沙蜥样本于2015年8月采集后剪趾标记，分A、B两类(A基底使用黑沙石，B使用枯黄色沙石)饲养于兰州大学实验室。采用0.60 m×0.45 m×0.35 m (长×宽×高)的浅白色塑料盒围栏养殖，每个盒子下方铺上3–5 cm厚的沙石，沙石采集自样本自然种群生境。在白天，盒子内的部分区域可以受到阳光照射以供蜥蜴调节体温。此外，给蜥蜴提供充足的食物(黄粉虫幼虫)和饮水。将30条非黑化的草原沙蜥饲养于2个A盒，30条黑化的变色沙蜥饲养于2个B盒。部分样本移植

图1　沙蜥体色及体色测定点选择。(A)黑化的变色沙蜥采集自黑色基底的生境(上), 非黑化的草原沙蜥采集自枯黄色基底的生境(下); (B) M1至M12分别代表蜥蜴个体体色测量的12个部位, 包括头顶部中心(M1)、背部左上方(M2)、背部右上方(M3)、背中部左侧(M4)、背中部右侧(M5)、背部左下方(M6)、背部右下方(M7)、左前肢(M8)、右前肢(M9)、左后肢(M10)、右后肢(M11)和尾根部背侧(M12)。

Fig. 1　Body color of lizards and the selected sites for color measurement. (A) "Melanistic" *P. versicolor* were collected from black substrate habitat (above), "non-melanistic" *P. frontalis* were sampled from withered yellow substrate habitat (below); (B) M1–12 represent twelve color measuring sites for each lizard, including cranial center (M1), top left on the back (M2), top right on the back (M3), left side on the central back (M4), right side on the central back (M5), bottom left on the back (M6), bottom right on the back (M7), left forelimb (M8), right forelimb (M9), left hind limb (M10), right hind limb (M11), and tail root (M12).

实验后经处理用于后续分子实验。

1.2　体色测量

个体体色的测量涉及12个部位(图1)。采用荷兰Avantes公司生产的AvaSpec-2048光纤光谱仪进行测量, 该仪器由光谱仪主机AvaSpec-2048-USB2、光源AvaLight-DH-S、反射探头FCR-7UV400-2-ME、探头固定器RPH-1和白色漫射板WS-2等部件组成。光谱采样间隔为0.60 nm, 波段范围为200–1,100 nm (杨灿朝等, 2011), 涵盖了有鳞目及其捕食者鸟类300–700 nm的视觉范围(Bennett & Cuthill, 1994)。用探头固定器固定反射探头, 预热主机后用白色漫射板WS-2校准, 在垂直蜥蜴检测皮肤部位表面和距离约2 mm的位置测量发射光谱, 曝光时间设为100 ms。每个蜥蜴个体抓捕2天后测量1次, 生境互换移植饲养后第8、9、10天分别测量1次, 共测量4次。每次对所有个体的体色测量均在上午9–11点进行。

1.3　数据分析

光谱数据用配套软件AvaSoft 8.1提取和转换, 提取光谱范围为300–700 nm的光反射率值并用于后续分析。Origin8.0用于图形制作, SPSS20.0软件用于统计学分析。用配对*t*检验比较分析各部位初次测定的光反射率分别与第8、9、10天的光反射率之间的差异。描述性统计值用平均值±标准误表示, 显著性水平设置为$P < 0.05$。

2　结果

分析结果显示, 黑化的变色沙蜥与非黑化的草原沙蜥种群个体各部位光反射率均存在显著差异(M1: $t_{29} = 8.273$, $P < 0.001$; M2: $t_{28} = 9.239$, $P < 0.001$; M3: $t_{29} = 9.533$, $P < 0.001$; M4: $t_{28} = 10.089$, $P < 0.001$; M5: $t_{29} = 10.572$, $P < 0.001$; M6: $t_{26} = 11.959$, $P < 0.001$; M7: $t_{29} = 10.923$, $P < 0.001$; M8: $t_{18} = 5.192$, $P < 0.001$; M9: $t_{20} = 6.579$, $P < 0.001$; M10: $t_{19} = 6.959$, $P < 0.001$; M11: $t_{19} = 7.258$, $P < 0.001$; M12: $t_{18} = 9.010$, $P < 0.001$)。

经过基底环境互换饲养后发现沙蜥样本体色变化很轻微, 实际上肉眼难以识别判定, 更无法定量。黑化与非黑化沙蜥种群各部位4次光谱测定的反射率统计描述值见表1。配对*t*检验结果(表2)显示, 在黑化的变色沙蜥种群中, 背部区域(M2–M7)第1天的皮肤光反射率与环境移植饲养后第8天、第9天及第10天的皮肤光反射率均存在显著差异(M5第10天除外), 而其他部位移植饲养前后的皮肤光反射率并无显著差异; 非黑化的草原沙蜥种群中, 背部右上方(M3)区域第1天的皮肤光反射率与移植饲养后第8天及第9天的皮肤光反射率存在显著差

表1 黑化的变色沙蜥与非黑化的草原沙蜥各检测部位的反射率(平均值±标准误)
Table 1 Mean values of reflectivity of each site for both “melanistic” *P. versicolor* and “non-melanistic” *P. frontalis*

检测部位 Sites	非黑化草原沙蜥 “Non-melanistic” *P. frontalis*				黑化变色沙蜥 “Melanistic” *P. versicolor*			
	第1天 1st day	第8天 8th day	第9天 9th day	第10天 10th day	第1天 1st day	第8天 8th day	第9天 9th day	第10天 10th day
M1	1.89±0.18	2.10±0.19	2.18±0.22	2.31±0.20	0.27±0.05	0.45±0.08	0.29±0.06	0.38±0.07
M2	2.23±0.18	2.57±0.16	2.87±0.22	2.72±0.20	0.40±0.05	0.75±0.09	0.82±0.09	0.75±0.09
M3	2.52±0.19	3.24±0.23	3.20±0.18	3.12±0.23	0.48±0.05	0.95±0.11	0.83±0.11	0.83±0.11
M4	2.20±0.18	2.42±0.18	2.42±0.24	2.40±0.17	0.29±0.03	0.55±0.06	0.64±0.08	0.60±0.08
M5	2.48±0.16	2.27±0.18	2.25±0.16	2.27±0.15	0.44±0.07	0.72±0.09	0.65±0.07	0.58±0.06
M6	2.37±0.15	2.30±0.15	2.51±0.16	2.96±0.26	0.39±0.05	0.68±0.09	0.73±0.10	0.61±0.08
M7	2.60±0.18	2.37±0.17	2.60±0.19	2.52±0.17	0.41±0.05	0.74±0.13	0.66±0.07	0.66±0.08
M8	2.83±0.37	2.83±0.27	2.81±0.34	1.99±0.17	0.58±0.15	0.53±0.09	0.59±0.18	0.62±0.17
M9	2.83±0.29	2.57±0.33	2.78±0.41	2.61±0.47	0.47±0.16	0.59±0.14	0.54±0.07	0.48±0.07
M10	2.21±0.29	1.67±0.25	0.99±0.13	0.93±0.13	0.18±0.03	0.22±0.06	0.19±0.02	0.21±0.06
M11	2.23±0.26	2.72±0.42	1.87±0.24	1.96±0.27	0.24±0.05	0.28±0.04	0.22±0.03	0.45±0.16
M12	3.82±0.40	3.56±0.38	3.38±0.45	3.09±0.31	0.64±0.11	0.72±0.08	0.96±0.20	1.16±0.25

表2 黑化的变色沙蜥与非黑化的草原沙蜥各测量部位移植实验前后反射率的配对*t*检验
Table 2 Paired *t* test analyses on reflectivity for each site in lizards before and after transplantation

检测部位 Sites	非黑化的草原沙蜥 “Non-melanistic” *P. frontalis*			黑化的变色沙蜥 “Melanistic” *P. versicolor*		
	第1天vs.第8天 1st day vs. 8th day	第1天vs.第9天 1st day vs. 9th day	第1天vs.第10天 1st day vs. 10th day	第1天vs.第8天 1st day vs. 8th day	第1天vs.第9天 1st day vs. 9th day	第1天vs.第10天 1st day vs. 10th day
M1	$t_{28} = 1.085, P = 0.287$	$t_{27} = 1.346, P = 0.189$	$t_{27} = 1.742, P = 0.093$	$t_{28} = 1.660, P = 0.108$	$t_{28} = 1.659, P = 0.109$	$t_{27} = 1.646, P = 0.112$
M2	$t_{28} = 1.382, P = 0.178$	$t_{27} = 1.724, P = 0.096$	$t_{27} = 1.990, P = 0.057$	$t_{28} = 3.598, P = 0.001^*$	$t_{27} = 4.297, P < 0.001^*$	$t_{27} = 3.099, P = 0.005^*$
M3	$t_{28} = 2.376, P = 0.025^*$	$t_{27} = 3.773, P = 0.001^*$	$t_{27} = 1.828, P = 0.079$	$t_{27} = 4.385, P < 0.001^*$	$t_{27} = 3.051, P = 0.005^*$	$t_{27} = 2.995, P = 0.006^*$
M4	$t_{28} = 0.741, P = 0.465$	$t_{27} = 0.530, P = 0.600$	$t_{27} = 0.515, P = 0.611$	$t_{28} = 3.669, P = 0.001^*$	$t_{27} = 3.749, P = 0.001^*$	$t_{27} = 3.438, P = 0.002^*$
M5	$t_{28} = -0.644, P = 0.525$	$t_{28} = -0.909, P = 0.372$	$t_{27} = -1.476, P = 0.152$	$t_{28} = 2.473, P = 0.020^*$	$t_{28} = 2.205, P = 0.036^*$	$t_{27} = 1.611, P = 0.119$
M6	$t_{27} = -0.348, P = 0.731$	$t_{26} = 0.467, P = 0.644$	$t_{23} = 1.593, P = 0.126$	$t_{27} = -2.686, P = 0.012^*$	$t_{26} = -3.366, P = 0.002^*$	$t_{23} = 2.248, P = 0.035^*$
M7	$t_{28} = -1.010, P = 0.321$	$t_{28} = -0.383, P = 0.705$	$t_{27} = -0.759, P = 0.455$	$t_{28} = -2.472, P = 0.020^*$	$t_{28} = -2.891, P = 0.007^*$	$t_{27} = 2.686, P = 0.012^*$
M8	$t_{16} = -0.068, P = 0.947$	$t_{16} = -0.111, P = 0.913$	$t_{16} = -1.789, P = 0.095$	$t_{16} = -0.527, P = 0.606$	$t_{16} = -0.396, P = 0.698$	$t_{16} = -0.100, P = 0.922$
M9	$t_{17} = 0.059, P = 0.954$	$t_{17} = 0.552, P = 0.589$	$t_{17} = 0.126, P = 0.902$	$t_{17} = -0.208, P = 0.838$	$t_{17} = 0.005, P = 0.996$	$t_{17} = -0.229, P = 0.822$
M10	$t_{16} = -1.477, P = 0.162$	$t_{16} = -4.168, P = 0.001^*$	$t_{16} = -4.049, P = 0.001^*$	$t_{16} = 0.639, P = 0.533$	$t_{16} = 0.046, P = 0.663$	$t_{16} = 0.564, P = 0.582$
M11	$t_{16} = 1.092, P = 0.293$	$t_{16} = -0.899, P = 0.384$	$t_{16} = -0.259, P = 0.799$	$t_{16} = 0.349, P = 0.733$	$t_{16} = -0.405, P = 0.691$	$t_{16} = -1.018, P = 0.372$
M12	$t_{16} = -0.261, P = 0.798$	$t_{16} = -0.605, P = 0.555$	$t_{16} = -1.630, P = 0.125$	$t_{16} = 1.428, P = 0.175$	$t_{16} = -1.847, P = 0.086$	$t_{16} = 2.235, P = 0.051$

* $P < 0.05$.

异；左后肢(M10)区域第一天的皮肤光反射率与移植饲养后第9九天和第10天的皮肤光反射率存在显著差异；而其他部位移植饲养前后的光反射率并无显著差异。

3 讨论

我们的研究结果表明，黑化生境下的变色沙蜥体色显著深于非黑化枯黄色沙丘生境下生存的草原沙蜥。生境互换围栏移植实验结果表明，饲养1周后，黑化种群背部6个检测部位(M2–M7)的光反射率统计值显著升高，其他部位均无显著变化；而非黑化种群只有背部右上方和左后肢2个部位(M3和M10)的皮肤光反射率统计值发生显著变化，其他部位反射率并无显著变化。虽然一些部位有统计差异，但种群内样本体色变异程度非常轻微，甚至肉眼难以识别是否发生体色变化。

动物体色变异的机制主要有生理体色变异和形态体色变异两种(Devi & Adnan, 2009)。对基底颜色的匹配可以降低动物在外出活动时被捕食者及猎物发现的可能性(Merilaita et al, 2001; Stuart-Fox et al, 2003; Vignieri et al, 2010)，而短期内快速匹配基底颜色的能力主要依赖于色素颗粒的快速扩散与聚集(即生理体色变化)(Nery & Castrucci, 1997)。研究发现部分鱼类以及一些两栖爬行类动物中存

在着生理上的快速体色变化，并能在短时间内匹配基底颜色(Mäthger et al, 2003; Boback & Siefferman, 2010; Choi & Jang, 2014)。我们的研究发现，两种沙蜥群体自然体色变化存在显著差异($P < 0.05$)，相比于上述快速的生理体色变化，互换环境饲养1周至10天后沙蜥样本体色与饲养时所处的基底颜色依然存在很大差异，并且肉眼难以区分是否发生了显著的体色变化。这说明，对基底生境颜色的短期适应变化并不能解释不同基底色生境中两种沙蜥所具有的显著的自然体色差异。

此外，有研究发现，在人为制造的具有不同颜色深度的基底环境中，“浅色”动物个体的体色变化程度通常要比黑化个体大(Norris, 1965; Schlichting & Pigliucci, 1999; Rosenblum, 2004)，这是因为相比于“浅色”个体，黑化个体由于增加了皮肤黑色素的产量来匹配起初的黑化基底环境，在短期非黑化环境刺激下聚集和扩散黑色素颗粒的能力相对更弱。然而，我们对两种沙蜥生境互换实验结果却发现，黑化的变色沙蜥种群样本在短期内的体色显著变化部位比非黑化草原沙蜥种群多，表明变色沙蜥可能具有比草原沙蜥更强的体色变异能力。此外，两种沙蜥种群显著的自然体色变化并不是色素颗粒的快速扩散或聚集而形成，其色素积累或体色变化在个体发育过程中可能是一个渐进的过程。

本文只比较了成体样本，未对幼体与亚成体进行比较，但这种体色变化显然是不同群体对不同基底环境的长期适应而形成的稳定的变化。我们的研究还发现西藏沙蜥(*P. theobaldi*)低海拔种群没有腹部黑斑，而海拔4,200 m以上的种群出现腹部黑斑，且腹部黑斑面积随海拔上升显著变大，并认为这是对不同温度环境的一种热适应(Jin & Liao, 2015)。而本研究选择的两种沙蜥群体海拔分布相近，但基底颜色显著不同，各沙蜥群体体色保持与基底颜色相近，有利于其反捕食。

动物体皮肤黑化的程度跟黑色素细胞的活性相关(Alibardi, 2013)，一些动物表皮黑色素细胞层可能需要数天或数月时间将黑素体逐渐转移到邻近的角质细胞层从而使皮肤黑化(即形态体色变异)(Cooper & Greenberg, 1992)。少数研究表明，与黑色素合成通路密切相关的基因遗传变异可能在爬行动物体色变异中扮演重要角色(Rosenblum et al, 2004, 2010)。本研究表明，不同基底色生境中生存的2种沙蜥体色的显著差异并不是对基底生境颜色的短期适应改变，而更倾向于是受遗传与进化因素影响的形态体色变异，两物种体色表型分化明显，其差异体色表型已在各自然种群中稳定遗传，但潜在的影响机制还需要日后分子生物学与功能实验进一步揭示。

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